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Radiological Study of Wheat Monosomics. III. The Differential Survival Rate of 21 Monosomics and the Disomic to γ-Ray Irradiation†

Koichiro TSUNEWAKI*

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As a means of studying the genetic similarities and dissimilarities between the 21 wheat chromosomes, selfed seeds of 21 monosomic strains of a common wheat *Triticum aestivum* cv. Chinese Spring were irradiated with γ-rays (0–60 kR), and their survival rate was observed about 30 days after sowing. Results are as follows: (1) Monosomic strains are, in general, much more sensitive to γ-rays than is the disomic. (2) The three monosomic strains of the same homoeologous group tend to show the same degree of sensitivity; group 2 is the most sensitive, followed by group 1, 6, and 3, 4 and 5. Group 7 is as resistant as the disomic. (3) In some homoeologous groups, a remarkable difference was noticed among the three monosomic strains; groups 1, 3, 4 and 5. (4) The lowest dosage of γ-rays, at which an appreciable killing occurred, was: 35 kR in mono-5B; 40 kR in mono-2A, (probably 2B), 2D, 3A, 3B, 4A, 6A, and 6D; 45 kR in mono-1A, 1B, 1D, 4D, 5D, and 6B; and 50 kR in mono-3D, 4B, 5A, 7A, 7B, 7D, and the disomic. Functional differentiation of the homoeologous chromosomes are taking place at a different rate in the different homoeologous groups. (5) The differential killing of the 21 monosomics and the disomic by γ-rays was, to some extent, correlated with the frequency of nullisomics, the average seed weight, the length of the monosomic chromosomes, and the survival rate of non-irradiated material. All these factors combined, however, explained only about 50% of the difference observed among the 22 strains.

INTRODUCTION

Recently, the genetics of polyploid wheat has been greatly advanced by the use of a monosomic series, initially established in a common wheat variety, Chinese Spring,[1] and which is now available in many other varieties. One important problem is to estimate the genetic homology as well as the differentiation of so-called "homoeologous" chromosomes, which are assumed to have been differentiated from a common, ancestral chromosome.[1,2] This problem has been attacked from several directions, *i.e.* the synaptic affinity of homoeologous chromosomes in the meiosis of haploids[3] or nulli-5B plants,[4] the functional compensation between homoeologous chromosomes in nulli-tetrasomic plants,[5] and by a comparison of nullisomics[6] or of genes located on homoeologous chromosomes.[7] Reviewing these studies and other related results, Tsunewaki[8] concluded that the homoeologous chromosomes had differentiated at different rates, although they still retain strong genetic homology.

† Contribution from the Laboratory of Genetics, Faculty of Agriculture, Kyoto University, Kyoto, No. 386.
* 常脇恒一郎 : Laboratory of Genetics, Faculty of Agriculture, Kyoto University.

Tsunewaki and Heyne[9] suggested that a radiological study of monosomics would provide an additional experimental approach to this problem. Their result[10] of irradiating 16 monosomics with a moderate dosage of X-rays showed functional homology as well as divergence among some homoeologous chromosomes. As an extension of this work, a new experiment has been carried out, in which all 21 monosomics were irradiated with a wide range of γ-ray dosages. Their responses were observed and analyzed for the survival rate, seedling height and morphological variations in the R_1 generation. Only the results on the survival rate will be described here. The analysis was mainly focused on a comparison between three monosomics of the same homoeologous group, and on the factors responsible for their different responses.

MATERIALS AND METHODS

A monosomic series of *Triticum aestivum* cv. Chinese Spring ($n=21$), provided by the courtesy of Dr. E. R. Sears, was used. According to Sears,[11] 21 monosomic lines have been designated, *i.e.* mono-1A or mono-2B, by the homoeologous group and genome to which their monosomic chromosomes belong. About ten plants were cytologically examined in each monosomic line and the monosomics thus selected were used for seed production by open pollination.

This seed population contains di-, mono-, and nullisomics. For convenience's sake this mixed population, *e.g.* of mono-1A, will be called, hereafter, "mixed mono-1A". Frequencies of the mono- and nullisomics, respectively, in the mixed populations had been previously estimated for all the monosomic lines by Tsunewaki[12] and Sears.[1]

Dormant seeds of a disomic and 21 mixed monosomics were exposed to γ-rays from ^{60}Co at nine different total dosages; 0 (control), 10, 25, 30, 35, 40, 45, 50, and 60 kR. Dose rates were all the same, 5 kR per day. All material was carefully handled in the same way throughout the experiment, *i.e.* in regard to the field management of parental plants, the harvest and storage of seeds before and after irradiation, and the sowing of irradiated seeds.

The experimental design used was a split plot in a randomized block design, with three replications and 22 strains; the disomic and 21 mixed monosomics for units, and nine γ-ray treatments for subunits.

Number of seeds receiving the same treatment differed among the 22 strains. This is shown in Table I together with the average seed weight. Frequencies of the mono- and nullisomics, and the length of the monosomic chromosome, which had been estimated by previous workers, are also indicated.

Seeds were planted in flats two days after irradiation. The survival rate was recorded about 30 days after sowing, when the non-irradiated plants were at the fifth leaf stage. An analysis of variance was applied. Since the number of seeds available for the mixed mono-2B was very small, data on this strain have been excluded from the analysis. The differential radiosensitivity among the monosomics was statistically defined by the interaction between the genetic strains and γ-ray dosages.

The radiosensitivity of a pure monosomic population, *e.g.* mono-1A, was estimated by the following formula:

Table I. Number of Seeds Sown per Treatment, Average Seed Weight, Frequencies of Mono- and Nullisomics, and the Length of the Monosomic Chromosomes in a Disomic and 21 Mixed Monosomics

Strains		No. seeds/ treatment	Ave. seed wt. (mg)	Freq. of monosomics (%)*	Freq. of nullisomics (%)**	Length of the monosomic chromosome (μ)**
Mixed mono-1A		150	24.7	79.8	2.1	7.34
〃	1B	150	25.3	64.0	2.4	10.42
〃	1D	102	21.0	79.3	2.4	5.55
〃	2A	105	24.4	64.1	2.4	10.92
〃	2B	36	23.1	69.0	5.0	8.11
〃	2D	150	25.8	68.0	4.4	8.18
〃	3A	150	27.8	71.9	2.4	8.50
〃	3B	150	29.6	77.0	7.6	12.32
〃	3D	135	21.4	80.1	5.8	7.45
〃	4A	150	21.9	69.4	6.4	9.04
〃	4B	150	21.9	72.8	3.6	7.91
〃	4D	150	25.2	70.6	5.9	6.85
〃	5A	150	21.2	81.9	3.4	9.81
〃	5B	150	19.2	70.3	1.0	11.34
〃	5D	150	17.2	71.6	0.9	5.77
〃	6A	150	25.9	77.4	2.5	6.26
〃	6B	150	20.1	57.3	0.9	9.10
〃	6D	150	23.2	78.1	2.8	5.90
〃	7A	150	19.4	70.8	3.3	9.10
〃	7B	150	22.4	70.6	1.4	8.76
〃	7D	150	24.2	68.8	1.1	9.06
Disomic		150	27.5	0.0	0.0	—

* Including nullisomics[12)]
** Taken from Sears[1)]

$$X = \frac{A - qB}{p}$$

where

X=the estimated γ-ray damage to mono-1A
A=γ-ray damage to the mixed mono-1A
B=γ-ray damage to the disomics
p=the proportion of mono-1A (including nulli-1A) in the mixed mono-1A
q=the proportion of disomics in the mixed mono-1A, or $=1-p$

In this formula, the difference in radiosensitivity between the mono- and nullisomics is ignored because of the low frequency of the latter in the mixture. However, nullisomics are apparently much more sensitive than are monosomics and since the former's frequency differs among the 21 monosomic lines, the estimated sensitivity must be an approximation. With this limitation, the radiosensitivity of all 21 monosomics was estimated, and its correlations to the frequency of nullisomics, the average seed weight, the length of the monosomic chromosome, and the survival rate of the control were worked out.

RESULTS AND DISCUSSION

1. Survival Rate of the Mixed Monosomic Populations

Average survival rates of the disomic and 21 mixed monosomics for the different γ-ray dosages are summarized in Table II.

The killing effect of irradiation to the disomic first appeared at a dosage of 45 kR and increased at higher dosages. At 60 kR, most of the disomics were killed. The effect of irradiation on the mixed monosomics varied with the strain; some being as resistant as the disomic, while others were extremely sensitive. On the average, the killing effect on the mixed monosomics was more severe than that on the disomic as, for example, a decrease in the survival rate was recognized at a dosage of 35 kR.

An analysis of variance was carried out with the original data, that had been transformed, prior to the analysis, from percentage to angle. The result is shown in Table III.

This result indicates that different strains exhibit different radiosensitivities. Orthogonal subdivision of the sum of the squares for the interaction ($S \times D$) of two com-

Table II. Percentage of Survival for the γ-Rayed Disomic and 21 Mixed Monosomics at the 5th Leaf Stage

Strains		γ-ray dosages (kR)								
		0	10	25	30	35	40	45	50	60
Mixed mono-	1A	94.6	95.3	94.0	89.3	90.0	82.5	56.0	33.6	0.0
〃	1B	85.4	91.3	96.7	92.0	92.0	83.2	64.3	61.5	9.7
〃	1D	99.0	98.1	98.0	97.0	98.0	86.3	60.8	41.2	0.0
〃	2A	96.2	96.1	96.1	85.7	86.3	74.8	60.3	30.5	0.0
〃	2B	87.2	74.1	94.0	93.3	86.9	73.5	56.2	33.3	3.7
〃	2D	94.0	93.3	94.7	96.0	80.0	76.7	52.7	37.3	0.7
〃	3A	96.7	97.3	96.0	95.9	91.3	87.8	79.3	70.0	7.3
〃	3B	94.0	91.3	80.7	72.7	78.0	62.7	52.2	42.7	1.3
〃	3D	97.0	95.6	94.1	95.6	92.6	90.4	83.0	67.4	7.4
〃	4A	92.7	85.3	85.3	82.0	74.7	68.7	32.0	34.0	0.7
〃	4B	94.6	94.0	94.7	94.0	96.7	89.3	81.9	69.3	10.7
〃	4D	96.7	97.3	96.7	96.7	89.3	90.7	63.3	58.0	4.0
〃	5A	99.3	97.3	94.7	96.7	93.3	93.3	86.7	73.3	6.7
〃	5B	93.3	97.3	92.0	89.3	74.7	73.8	64.7	48.0	4.7
〃	5D	99.3	98.0	98.7	90.7	93.3	91.3	66.0	54.0	4.0
〃	6A	94.0	97.3	94.0	88.7	81.3	73.3	68.7	57.3	6.0
〃	6B	95.3	99.3	92.7	91.3	95.3	94.6	70.0	63.1	4.7
〃	6D	96.0	98.7	96.7	94.0	84.7	83.3	64.7	58.7	2.7
〃	7A	97.3	96.0	92.0	98.7	92.6	90.0	82.7	60.7	4.7
〃	7B	94.0	92.0	98.0	94.0	92.0	90.7	80.0	66.0	2.7
〃	7D	97.3	98.0	97.3	97.3	91.9	92.0	74.0	57.3	2.0
Disomic		99.3	97.3	98.7	98.7	96.7	98.0	90.7	77.3	4.7
Ave. of mixed monos.		95.3	95.4	94.2	91.9	88.4	83.8	67.2	54.2	4.0
Exp. pure monos.*)		94.0	94.8	92.6	89.6	85.6	79.0	59.3	46.4	3.8

*) Assuming that the progeny of the monosomics consist of 25% disomics and 75% monosomics.

Table III. Analysis of Variance for the Survival Rate of γ-Rayed Disomic and 21 Mixed Monosomics at the 5th Leaf Stage

Source of variation	df	Sum of the squares	Mean square	F-value
Total	566	305, 169. 32		
Units				
Replications (R)	2	404. 81	202. 404	1. 382$^{N.S.}$
γ-ray dosages (D)	8	267, 272. 24	33, 409. 030	228. 160**
Error a	16	2, 342. 84	146. 428	
Subunits				
Strains (S)	20	14, 164. 99	708. 249	25. 331**
$S \times D$	160	10, 918. 95	68. 244	2. 441**
Error b	360	10, 065. 48	27. 960	
Subdivision of $S \times D$				
Disomic *vs* mixed monosomics	8	766. 36	95. 794	3. 426**
Among mixed monosomics	152	10, 152. 60	66. 793	2. 389**
Among homoeologous groups	48	3, 677. 24	76. 609	2. 740**
Among monosomics of the same group	104	6, 475. 36	62. 263	2. 227**

N.S. and **: Non-significant and significant at the 1% level, respectively.

ponents, *i.e.* disomic *vs* mixed monosomics, and within the latter revealed that the radiosensitivity of the mixed monosomics, as the whole, was significantly higher than that of the disomic, also that the radiosensitivities of different mixed monosomics significantly differ.

2. Difference among the Seven Homoeologous Groups

The sum of the squares of the latter component was further subdivided into two components; those attributable to the homoeologous group and to those attributable to mixed monosomics within the same homoeologous groups. The result shown in the last two lines of Table III indicates that more than one-third of the sum of the squares is due to differential sensitivity among the different homoeologous groups. The mean square attributable to the interaction for inter-homoeologous groups was 76.6 (significant at the 0.1 per cent level), while that for the within-groups was 62.3 (also, significant at the 0.1 per cent level). From this we see that each homoeologous group strongly retains the characteristic pattern of its radiological response, even though significant differentiation has occurred among some homoeologous chromosomes. For example, all three monosomics of group 7 were as resistant as the disomic, while the monosomic lines of group 2 were all very sensitive.

3. Difference among Three Monosomics Belonging to the Same Homoeologous Groups

To clarify the similarity or dissimilarity of the radiological response of three monosomics belonging to the same groups, the sum of the squares for the interaction, $S \times D$, was calculated for each homoeologous group; including the disomic for comparison. When the interaction between mixed monosomics of the same group was significant, the sum of the squares was conventionally subdivided to make a significant comparison. Results are summarized in Table IV.

Table IV. Subdivision of the Sum of the Squares for the Interaction, $S \times D$, to the Seven Homoeologous Groups, and Further Subdivisions for Significant Comparisons

Homoeologous group	Source of variation	df	Sum of the squares	Mean square
	Error b	360	10,065.5	27.96
Group 1	Total	24	2,776.9	115.71**
	Disomic *vs* monosomics	8	918.4	114.80**
	Within monosomics	16	1,858.6	116.16**
	Mono-1B *vs* mono-1A & -1D	8	1,626.2	203.27**
	Mono-1A *vs* mono-1D	8	232.4	29.05 N.S.
Group 2	Total	16	1,445.4	90.34**
	Disomic *vs* monosomics	8	1,106.6	138.32**
	Within monosomics	8	338.8	42.35 N.S.
Group 3	Total	24	1,264.7	52.69**
	Disomic *vs* monosomics	8	718.8	89.84**
	Within monosomics	16	545.9	34.12 N.S.
	Mono-3B *vs* disomic & mono-3A, -3D	8	740.6	92.58**
	Among disomic, mono-3A & -3D	16	524.0	32.75 N.S.
Group 4	Total	24	1,849.5	77.06**
	Disomic *vs* monosomics	8	716.2	89.53*
	Within monosomics	16	1,133.2	70.83*
	Mono-4A *vs* disomic & mono-4B, -4D	8	1,076.7	134.59**
	Among disomic & mono-4B, -4D	16	772.8	48.30 N.S.
Group 5	Total	24	1,922.4	80.10**
	Disomic *vs* monosomics	8	715.1	89.38**
	Within monosomics	16	1,207.3	75.46**
	Disomic & mono-5A *vs* mono-5B & -5D	8	1,135.4	141.93**
	Disomic *vs* mono-5A	8	215.9	26.99 N.S.
	Mono-5B *vs* mono-5D	8	571.0	71.38**
Group 6	Total	24	1,575.2	65.63*
	Disomic *vs* monosomics	8	838.7	104.84**
	Within monosomics	16	736.5	46.03 N.S.
Group 7	Total	24	860.6	35.86 N.S.
	Disomic *vs* monosomics	8	205.7	25.71 N.S.
	Within monosomics	16	654.9	40.93 N.S.

N.S., *, and **: Non-significant, and significant at the 5% and 1% level, respectively.

Homoeologous group 1: Mixed monosomics of this group, as a whole, showed a higher sensitivity than did the disomic. Among the three monosomics, no difference was found between mixed mono-1A and -1D, while mixed mono-1B was more resistant than both. The order of their radiosensitivity can be expressed as follows:

disomic<mono-1B<mono-1A=mono-1D.

Homoeologous group 2: Two mixed monosomics, mono-2A and -2D, of this group showed a much higher sensitivity than did the disomic. No difference was found between them. Based on the limited data, mixed mono-2B appears to have a sensitivity of the same degree as mixed mono-2A and -2D. The order of their sensitivity is as follows:

disomic<mono-2A=mono-2D (=mono-2B).

Homoeologous group 3: Conventional subdivision of the sum of the squares indicated that the mixed monosomics of this group, as a whole, are more sensitive than the disomic, and that no differences exist among the three monosomics. Another but more significant subdivision of the sum of the squares was worked out; the result is that mono-3B is more sensitive than the disomic, while mono-3A and -3D are almost as resistant as the disomic. Their relationship can be expressed as follows:

disomic=mono-3A=mono-3D<mono-3B.

Homoeologous group 4: Conventional analysis indicated that the mixed monosomics, on the average, are more sensitive than the disomic and that a significant difference exists between the monosomics. To clarify this result, another subdivision of the sum of the squares was carried out. The result indicated that mono-4A is more sensitive than the disomic, while two others, mono-4B and -4D, are as resistant as the latter. Their relationship, therefore, can be shown as follows:

disomic=mono-4B=mono-4D<mono-4A.

Homoeologous group 5: Conventional analysis indicated that two comparisons; one between the disomic *vs* mixed monosomics and one within the monosomics were significant. Another subdivision clearly showed that the disomic and mono-5A are similar in radiosensitivities, while mono-5B and -5D are more sensitive than the disomic; the former being more so than the latter. Thus, their relation can be expressed as follows:

disomic=mono-5A<mono-5D<mono-5B.

Homoeologous group 6: Subdivision of the sum of the squares revealed that the mixed monosomics were more sensitive than the disomic, and that no difference existed among the three monosomics. Their relation, therefore, can be written as follows;

disomic<mono-6A=mono-6B=mono-6D.

Homoeologous group 7: Conventional analysis revealed that the radiosensitivities of the three monosomics and the disomic did not significantly differ. This relation can be expressed as follows:

disomic=mono-7A=mono-7B=mono-7D.

It is uncertain from present results what portion of the differential killing of the monosomics is strictly genetic and what is physiological in nature. Materials used in this study were carefully handled under the same conditions. However, the physiological condition of the seeds must differ, *e.g.* the moisture content or degree of weathering of the grains might vary among the 21 monosomic lines, because some lines mature later than others. Tightness of the glumes would also differ. These characters are undoubtedly hereditary, being specific to some monosomics. The differential radiosensitivity caused by these physiological differences can be considered, in a broad sense, to be under the control of the genotype of each monosomic line.

By accepting that the observed differential radiosensitivity of the monosomics is mainly associated with hemizygous chromosomes, one can radiologically estimate the degree of functional homology among the homoeologous chromosomes. The homology among the three homoeologous chromosomes, revealed by similar killing responses to irradiation, can be statistically evaluated with the mean square attributable to the interaction between γ-ray dosages and the three monosomic lines of the same homoeologous group. This within-group differentiation of chromosomes was most pronounced in homoeologous group 1, (M. S.=116.16**), followed by group 5 (M. S.=75.46**) and group 4 (M. S. =70.83*). By a further subdivision of the sum of the squares, some significant differentiation was also detected in group 3. No significant differentiation was found in group 2 (M. S.=42.35), group 6 (M. S.=46.03), and group 7 (M. S.=40.93). This clearly shows that the functional differentiation of homoeologous chromosomes occurred at different rates in different homoeologous groups.

4. Estimation of the Lowest Dosage with Which Each Monosomic Strain Showed Higher Killing Rate than the Disomic

The actual mean survival rate of each strain at a specific dosage can be adjusted with the mean survival rates of the respective strain and that of the respective dosage. With these adjusted mean survival rates, one can compare any two strains for their radiosensitivities at each dosage. To find out which dosage caused the differential killing of

Table V. Difference in the Adjusted Mean of the Survival Rate for Mixed Monosomics from That for Disomic (Transformed to Angle)†)

Strains		γ-ray dosages (kR)								
		0	10	25	30	35	40	45	50	60
Mixed mono-	1A	+ 4.1	+ 9.3*	+6.2	−0.8	+ 4.3	− 5.1	−10.2*	−11.9**	+ 4.2
〃	1B	− 9.2*	+ 0.7	+5.4	−1.9	+ 2.7	− 7.3	− 9.4*	+ 0.5	+18.1**
〃	1D	+ 7.1	+ 8.6*	+8.4	+3.5	+11.2*	− 8.4	−14.0**	−14.1**	− 2.5
〃	2A	+ 6.3	+13.1**	+8.9	−3.6	+ 1.8	−10.2*	− 7.4	−13.6**	+ 4.5
〃	2D	− 3.8	+ 7.7	+7.2	+7.2	− 3.2	− 9.3*	−11.8**	− 9.3*	+ 7.2
〃	3A	− 0.4	+ 7.4	−0.4	−0.1	− 3.3	−10.1*	− 3.9	+ 0.7	+ 9.7*
〃	3B	+ 9.0*	+ 9.6*	−1.4	−8.2	− 0.4	−13.6**	− 7.5	− 1.6	+14.5**
〃	3D	− 0.7	+ 1.9	−2.2	−1.7	− 1.0	− 6.8	− 1.0	± 0.0	+11.2**
〃	4A	+10.6*	+ 5.9	+3.6	−0.5	− 1.2	− 8.6*	−18.1**	− 5.5	+13.2**
〃	4B	− 4.5	± 0.0	−1.1	−1.5	+ 4.0	− 7.6	− 1.6	+ 0.9	+11.0*
〃	4D	+ 0.1	+ 7.8	+3.1	+3.0	− 1.5	− 4.8	−12.4**	− 4.2	+ 8.5*
〃	5A	+ 3.3	+ 1.5	−4.6	−1.5	− 0.2	− 6.8	− 1.0	+ 0.7	+ 7.8
〃	5B	+ 1.2	+15.1**	+2.3	−2.0	− 8.6*	−12.6**	− 6.0	− 4.6	+15.0**
〃	5D	+ 7.1	+ 6.4	+7.1	−6.3	+ 0.6	− 4.9	−11.6**	− 7.2	+ 8.2
〃	6A	+ 2.7	+11.6**	+3.4	−4.2	− 5.7	−14.7**	− 5.4	− 0.9	+13.0**
〃	6B	− 2.9	+11.3**	−0.9	−6.2	+ 2.8	− 0.9	− 9.4*	− 2.4	+ 8.4
〃	6D	+ 1.2	+11.8**	+6.6	−0.2	− 4.5	− 9.1*	− 9.1*	− 1.8	+ 5.1
〃	7A	+ 1.5	+ 2.4	−4.7	+6.3	− 1.1	− 7.3	− 0.8	− 4.2	+ 7.6
〃	7B	− 3.6	− 1.6	+4.6	−2.7	− 0.9	− 5.5	− 2.4	+ 7.3	+ 4.8
〃	7D	+ 2.0	+ 7.6	+4.7	+2.8	− 1.6	− 4.7	− 6.7	− 5.8	+ 1.2

†) (disomic)−(mixed monosomic)
Note) 5% l. s. d.=8.5, and 1% l. s. d.=11.2

Table VI. Classification of 21 Mixed Monosomic Strains on the Basis of Differential Radiosensitivity

Homoeologous group	First differed from the disomic at dosage			Not differing from the disomic	Order of radiosensitivity assumed from the results of Table IV
	35 kR	40 kR	45 kR		
1			1A, 1B, 1D		1A=1D>1B>di
2		2A, 2D, (2B)			2A=2D(=2B)>di
3		3A, 3B		3D	3B>3A=3D=di
4		4A	4D	4B	4A>4D=4B=di
5	5B		5D	5A	5B>5D>5A=di
6		6A, 6D	6B		6A=6D=6B>di
7				7A, 7B, 7D	7A=7B=7D=di

monosomics, from the disomic, the difference between the adjusted mean survival rate of the mixed monosomics and that of the disomic was calculated for each dosage, as shown in Table V. The least significant difference was estimated from the sum of the squares for the interaction, $S \times D$, in Table III.

Results presented in Table V indicate that the differential killing occurs at more or less different γ-ray dosages in different monosomic lines. From the dosage, at which the

Table VII. Relative Survival Rate for the 21 Pure Monosomics Exposed to γ-Ray Irradiation

Strains	γ-ray dosages (kR)								
	0	10	25	30	35	40	45	50	60
Mono-1A	100	101.5	99.4	93.1	94.6	84.2	50.6	24.1	0.0
〃 1B	100	113.3	123.2	113.7	115.2	96.5	63.7	67.8	16.1
〃 1D	100	99.4	98.9	97.7	99.4	84.1	53.6	32.1	0.0
〃 2A	100	100.9	100.1	82.9	85.2	65.4	45.8	4.5	0.0
〃 2B	100	77.8	112.3	111.1	100.8	76.4	49.7	16.5	4.0
〃 2D	100	99.9	101.4	103.5	78.8	72.9	38.0	20.2	0.0
〃 3A	100	101.7	99.2	99.1	93.2	87.6	78.2	70.1	8.7
〃 3B	100	96.8	81.5	70.2	78.3	56.4	44.0	35.1	0.3
〃 3D	100	98.7	96.4	98.3	95.0	91.8	84.1	67.3	8.4
〃 4A	100	89.1	88.5	83.1	72.4	62.2	6.8	16.6	0.0
〃 4B	100	100.0	100.5	99.4	104.2	92.7	84.7	71.5	13.9
〃 4D	100	101.8	100.3	100.3	90.2	91.7	54.3	52.3	3.9
〃 5A	100	98.0	94.5	97.0	93.1	92.9	86.4	72.9	7.1
〃 5B	100	107.1	98.2	93.9	72.0	70.0	59.1	39.2	5.2
〃 5D	100	99.0	99.4	88.1	92.6	89.2	56.6	45.0	3.7
〃 6A	100	105.2	100.1	92.7	83.0	71.5	67.3	55.7	6.9
〃 6B	100	108.3	95.5	92.9	102.1	99.7	59.1	56.9	5.1
〃 6D	100	104.3	101.1	97.5	85.5	83.3	60.4	56.3	2.2
〃 7A	100	98.9	92.4	102.3	94.2	89.8	82.3	55.8	4.9
〃 7B	100	97.8	106.4	100.2	98.0	95.5	82.2	66.8	2.1
〃 7D	100	101.9	100.3	100.3	93.0	92.6	68.9	50.0	0.8
Disomic	100	98.0	99.4	99.4	97.4	98.7	91.3	77.8	4.7

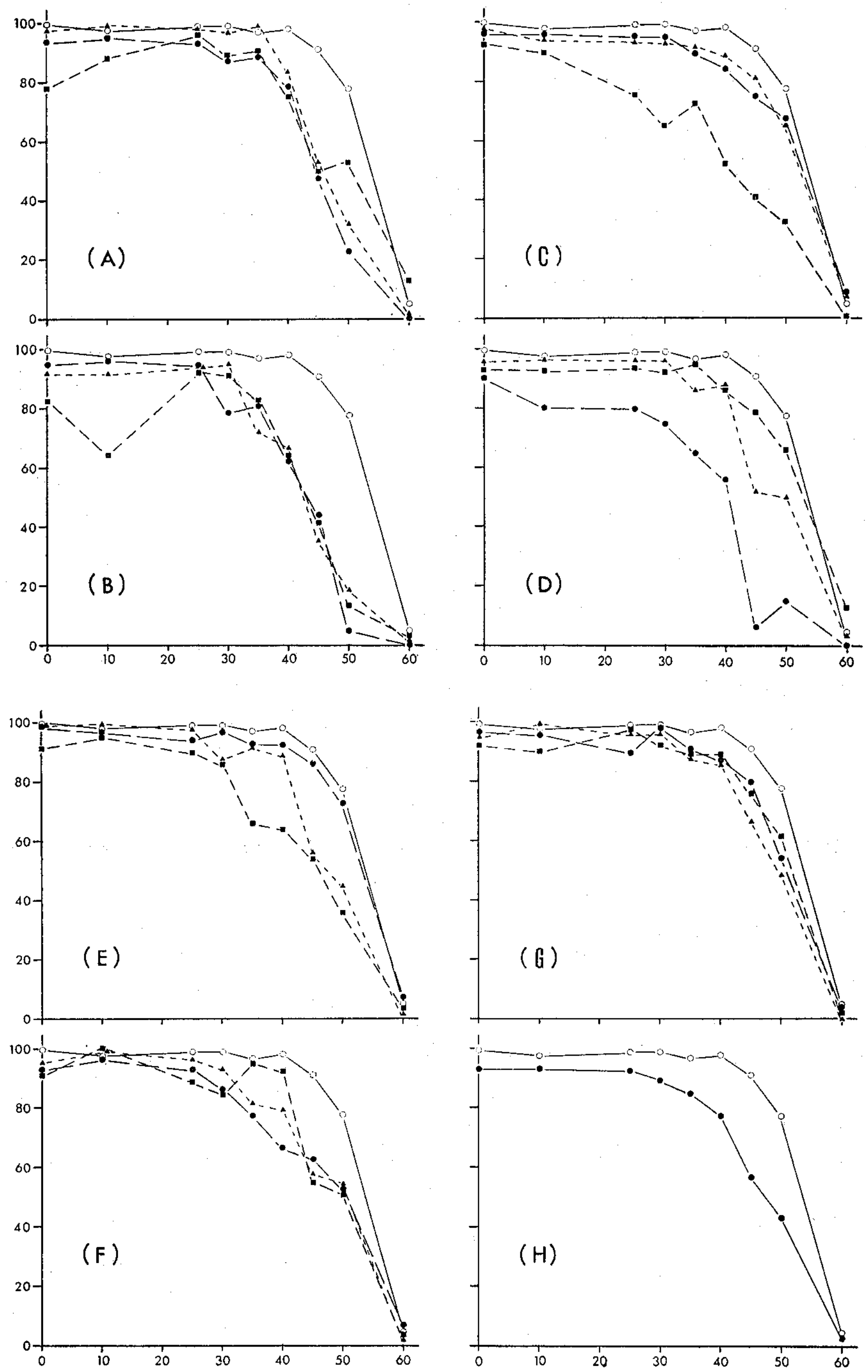

Fig. 1. Estimated survival rate of the pure monosomics and disomic (Each monosomic strain is indicated by the homoeologous group and genome to which the monosomic chromosome belongs). (A)–(G): The disomic and three pure monosomic strains of homoeologous groups 1–7, respectively. (H): The disomic and the average of the 21 monosomic strains. –○–, –●–, – –■– –, and ----▲-----: The disomic strain, and the monosomic strains of the A, B and D genome, respectively.

differential killing occurred, 20 monosomic lines were classified as shown in Table VI, together with results obtained from the subdivision of the sum of the squares for the interaction, $S \times D$, within each homoeologous group.

Results obtained by two different but interrelated methods were in good agreement with the exception of mixed mono-3A. The sensitivity of this strain did not differ from that of the disomic, when the subdivision of the sum of the squares for the interaction was carried out. In contrast the test of the difference of the adjusted means indicated that the sensitivity of this monosomic at 40 kR was significantly higher than that of the disomic. In this case, the result obtained by the former method seemed plausible.

Combining all this information, it can be said that the three mixed monosomics in each of the homoeologous groups, 2, 7 and probably 6, show similar radiological responses, while, at least, one member of the other groups is differentiated from its homoeologues.

5. Estimated Survival Rate of the 21 Pure Monosomics

From the formula presented in "Materials and Methods", the survival rates of 21 pure monosomics were estimated using the data presented in Table II. The estimated survival rate for each monosomic strain is shown in Figure 1. To make the comparison easy, three monosomics of the same homoeologous group were put together with the disomic. Looking at the figure, the results compiled in Table VI are confirmed.

The estimated survival rate of γ-irradiated monosomics was compared to that of the respective, non-irradiated monosomics; the ratio is expressed in percentage and is called hereafter "the relative survival rate". This relative survival rate, that can be considered as an index of the radioresistance exhibited by a given strain at a certain dosage, was calculated for each monosomic strain, and is shown in Table VII.

6. Contributions of Four Factors to the Differential Sensitivities of the 21 Monosomics

It is already evident that there is a differential radiosensitivity among the 21 monosomic lines. To determine what factors are responsible for this differential radiosensitivity, correlations were worked out between the relative survival rate and four characters, that were assumed to have some relation to sensitivity. These were frequency of nullisomics, average seed weight, length of the monosomic chromosome, and the survival rate of the non-irradiated monosomics. In this analysis, data for three dosages; 10, 25, and 60 kR, were excluded, because the monosomics and the disomic did not show much of a significant difference in their sensitivities at those dosages. Results are summarized in Table VIII.

The correlation was consistently negative between the relative survival rate and the frequency of nullisomics. It became highly significant when all the data were pooled. The differential radiosensitivity observed among the monosomics can be, in part, explained by the different frequencies of the nullisomics mixed in them. Evidently, a monosomic line containing a large proportion of nullisomics shows a higher radiosensitivity than does one with fewer nullisomics. This is reasonable, because the nullisomics must be much more sensitive than the monosomics. Note, however, that the degree of correlation was at a maximum at 40 kR, and gradually decreased at higher dosages. This indicates that the differential killing of the nullisomics became less important at higher dosages.

Table VIII. Correlation of the Relative Survival Rate of the γ-Rayed Monosomics to the Frequency of Nullisomics, the Average Seed Weight, the Length of the Monosomic Chromosome and the Survival Rate of the Control

Factors tested for correlation	Relative survival rate at				
	30 kR	35 kR	40 kR	45 kR	50 kR
Freq. of nullisomics	−.237	−.292	−.448	−.352	−.254
Length of mono. chromosome	−.279	−.194	−.328	−.082	−.112
Average seed wt.	−.124	−.129	−.357	−.173	−.101
Survival rate of control	−.379	−.250	+.133	+.270	+.154

A consistent negative correlation was also found between the relative survival rate and the length of the monosomic chromosome. The correlation was significant in the data pooled for the three lower dosages, which suggests that a plant lacking a large chromosome is more sensitive than one deficient in a small chromosome. It is not surprising from the genetic standpoint, because the hemizygous state for a large chromosome must cause more severe radiological damage to plants. The correlation between the relative survival rate and the average seed weight was also consistently negative. This is rather unexpected, because a well developed endosperm, which is the major constituent of wheat grain, seems to result in better recovery from radiation damage. At present, this can not be explained with any certainty, unless we assume that a large seed has a large embryo with a large target.

The survival rate of the non-irradiated monosomics can be considered to represent the general vitality of the respective monosomic lines. Thus, it is worth testing the correlation of this to the relative survival rate of the irradiated plants. The correlation was negative at two lower dosages, becoming positive at the three higher dosages. This can be interpreted as follows: The higher vitality of the monosomics is, in general, associated with higher radioresistance, resulting in a positive correlation between the survival rate of non-irradiated monosomics and the relative survival rate of irradiated ones. At the lower dosages (0–35 kR), however, spontaneous seed death, which is not related to the genetic weakness of each monosomic line, is of relative importance. If this spontaneous death occurred in the control (non-irradiated) of any of the monosomic lines, then those lines would show an apparent high tolerance to the low dosages of irradiation, and *vice versa*, when the relative survival rate is used as the measure. This is a plausible explanation for the negative correlation observed between the survival rate of non-irradiated monosomics and the relative survival rate of the weakly irradiated ones.

To evaluate the relative importance of these factors on the differential radiosensitivity, a multiple correlation and the standard partial regression coefficients were worked out between the relative survival rate and the above four factors. Since the highest simple correlation was usually obtained at a dosage of 40 kR, data for this dosage were chosen as the model for the analysis. The results were:

$$b'_{YX_1 \cdot X_2X_3X_4} = -0.3512$$

$$b'_{YX_2 \cdot X_1X_3X_4} = -0.2546$$

$$b'_{YX_3 \cdot X_1X_2X_4} = -0.1665$$

$$b'_{YX_4 \cdot X_1X_2X_3} = -0.0445$$

$$R = 0.5426$$

Where,

b'=the standard partial regression coefficient,

X_1=frequency of nullisomics,

X_2=the length of the monosomic chromosome,

X_3=average seed weight,

X_4=the survival rate of non-irradiated monosomics,

Y=the relative survival rate of monosomics at 40 kR,

and, R=the multiple correlation of Y to four X's.

Results indicate that the relative contributions of the four factors, X_1, X_2, X_3, and X_4, are if they really exist, in a ratio of about 8 : 6 : 4 : 1 in that order, and that the total contribution of the four explains only half of the differential radiosensitivity observed at this dosage. At higher dosages, where more distinct differential radiosensitivity was observed, the contribution of these known factors is assumed to be much smaller. Evidently, unknown factors play at least as important a role as do the factors discussed here.

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